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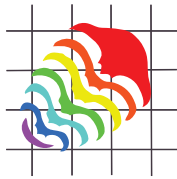
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Bessarabian (Tortonian, Late Miocene) fish otoliths from a transitional freshwater-brackish environment of Mykhailivka, Southern Ukraine

Andriy Bratishko, Oleksandr Kovalchuk, and Werner Schwarzhans

ABSTRACT

The Mykhailivka sedimentary section in southern Ukraine of middle (Bessarabian) to late (Khersonian) Sarmatian *s.l.* age is well known for its rich vertebrate finds in alternating marginal marine to estuarine and lacustrine environments. Here we describe fish otoliths obtained from sediments from a supposedly estuarine environment that had already yielded fossil fish bones and teeth described earlier. The otolith association is dominated by three species of gobiids, which are all related to the endemic extant Ponto-Caspian gobiid fauna. One species – *Neogobius bettinae* n. sp. – is described here. Rare associated species are *Morone* cf. *nobilis*, so far only known from the North Sea Basin, and a sciaenid. All otolith-based species represent euryhaline groups of fishes that are known today to commonly migrate from marine into brackish waters or are adapted to brackish and freshwater environments.

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INTRODUCTION

During the Middle Miocene the Paratethys ocean became gradually isolated from the world oceans with only transient connectivity (Rögl, 1998). The Central and Eastern Paratethys seas were interconnected during short-lived transgressive events in the Konkian (late Badenian) and Early Sarmatian (Volhynian) during which times fully marine conditions prevailed, while the increasing degree of separation overall triggered a gradually decreasing of salinity (Popov et al., 2004; Ilyina, 2006; Ter Borgh et al., 2014). During the Late Miocene, a restricted marine environment continued to prevail in the Eastern Paratethys while the Central Paratethys developed into the brackish / freshwater Pannonian Sea (Popov et al., 2004).

Here we describe otoliths from a mixed riverine / marginal marine environment from the

Bessarabian, Middle Sarmatian s.l. (Tortonian) of Mykhailivka, Southern Ukraine, which during that time was located near the northwestern edge of the former Eastern Paratethys (Figure 1). The fish fauna is composed of pharyngeal teeth of ostariophysans, as well as jaw teeth and bones of other freshwater fishes described earlier by Kovalchuk (2015), and non-ostariophysan otoliths described here. The otolith assemblage contains five species belonging to four genera in three families: Moronidae, Sciaenidae, and Gobiidae. In the sampled interval, the fish fossils were associated with marine and non-marine molluscs as well as terrestrial mammal remains indicating the mixed nature of the sedimentary environment (Prisyazhniuk et al., 2006). It is one of the few freshwater to brackish otolith-based fish faunas known from the early to middle Sarmatian s.l. and equivalents of the Paratethys (Weinfurter, 1952, 1954; Rückert-



FIGURE 1. Map of Ukraine with the coastline of Eastern Paratethys (blue line) during the late middle Sarmatian s.l. (according to Popov et al., 2004) (1), enlarged part of the lower reaches of the Pivdennyi Buh River (2), location map of the Mykhailivka quarry (3). The Mykhailivka locality is marked by an asterisk.

Ülkümen, 1996; Rückert-Ülkümen et al., 1993, 2006). Other coeval otolith associations stem from marine or restricted marine environments, e.g., Weiler (1943), Pobedina (1954), Strashimirov (1984, 1985), and Djafarova (2006). The same is true for fish faunas based on articulated skeletons, sometimes with otoliths in situ, e.g., Carnevale et al. (2006), Bannikov (2010), Bannikov and Kotlyar (2015), Schwarzhans et al. (2017a, 2017b, 2017c).

Here we apply the term “Sarmatian s.l.” (Hilgen et al., 2012) to indicate the Sarmatian of the Eastern Paratethys, and we use the traditional terms “Bessarabian” and “Khersonian” which are Middle and Upper Sarmatian, accordingly (Muratov and Nevesskaya, 1986).

Geological Setting

The studied fish remains were collected in the northern Mykhailivka quarry (47°39'06.75"N, 31°57'10.09"E) on the left bank of the Pivdennyi Buh River near the village of Mykhailivka (Mykolaiv region, Southern Ukraine) (Figure 1). This quarry has been well known for its fossil content since the late 1970s (Gozhik and Prisyazhniuk, 1978 – gastropods; Prisyazhniuk and Kovalenko, 2002 – bivalves, gastropods and ostracods; Topachevsky et al., 1997; Nesin and Nadachowski, 2001, Nesin, 2013 – all dealing with small mammals). Prisyazhniuk et al. (2006) provided a detailed description of the profile including taxonomic, ecological, and stratigraphic information based on bivalves, gastropods, nannofossils, and spore-pollen assemblages. Accordingly, the Miocene sequence starts with a middle Sarmatian s.l. coquina unconformably overlying Eocene carbonates. The section is about 35 m thick and composed of clays and siltstones, with minor interbedded limestones and sands, and comprises seven transgressive-regressive cycles (Figure 2). Each cycle begins with a thin nearshore marine or lagoonal phase, often carbonate and oolitic in nature, overlain by a succession of riverine and lacustrine freshwater and terrestrial root-bearing beds. Prisyazhniuk et al. (2006) gave a detailed account of the changing faunal composition of lamellibranchiates (*Mastra* beds in the marine zone), gastropods, ostracods, and plant remains. The environmental setting is interpreted here as a coastal lowland close to the Sarmatian Sea. Small low energy rivers crossed the plain and entered to the sea possibly in small estuaries, since there are no indications of channelized or river bar bedding structures. The individual cycles could represent phases of minor sea level fluctuations as would be expected in an

enclosed basin, similar to the modern Caspian Sea. The stratigraphical correlation is mainly based on mollusc and ostracod data, as well as on the recognition of the mammal zones MN10 and MN11, and comprises the stratigraphic interval from the upper Bessarabian (upper middle Sarmatian s.l.) to the lower Khersonian (lower upper Sarmatian s.l.) (Prisyazhniuk et al., 2006; Kovalenko, 2012; see Figure 2).

The fish otoliths described here were collected from the lower part of the section (layers 6-9 = M.1 = Mykhailivka 1; Figure 2). This represents a level particularly rich in mammal fossils and an unusual mixture of marine and freshwater taxa (Prisyazhniuk et al., 2006), and may represent a short-lived estuarine environment in our assessment. Pharyngeal teeth of carp fishes (Ostariophysi) and fish bones of other freshwater fishes obtained from this level (M.1) as well as a higher level in the section (layer 25 = M.2 = Mykhailivka 2) were studied by Kovalchuk (2015). The small mammal fossils facilitated a stratigraphic assignment of M.1 to the mammal zone MN10, and of M.2 to the mammal zone MN11 (Topachevsky et al., 1997; Nesin, 2013), which is consistent with the ages based on molluscs and ostracods. However, nannofossils from layer 15 have been determined as NN 8 (Prisyazhniuk et al., 2006). Thereby the nannoplankton is somewhat older than MN 10 (see Hilgen et al., 2012 for details) and in our view it could be a reworked assemblage.

MATERIAL AND METHODS

The studied screen-washed material was collected by V. Topachevsky, L. Rekovets, and V. Nesin (National Museum of Natural History, National Academy of Sciences of Ukraine, Kyiv) during their field campaigns in the 1980s. About 700 kg of sediments from M.1 were processed using a 1 mm mesh. Among many other fossils, the residue also contained thirty otoliths. The collection is housed in the Department of Paleontology, National Museum of Natural History NAS of Ukraine, Kyiv; acronym NMNHU-P. The ichthyological systematics in this paper follows Nelson (2006). The identification of otoliths is based on the literature and comparative collections of one of us (Werner Schwarzhans) and specimens in the National Museum of the Natural History NAS of Ukraine no. 2532, Zoological Museum of Moscow University (ZMMU) and Weinfurter's (1954) collection housed in the Department for Earth and Environmental Sciences, Palaeontology and Geobiology, Ludwig-Maximilians-Universität

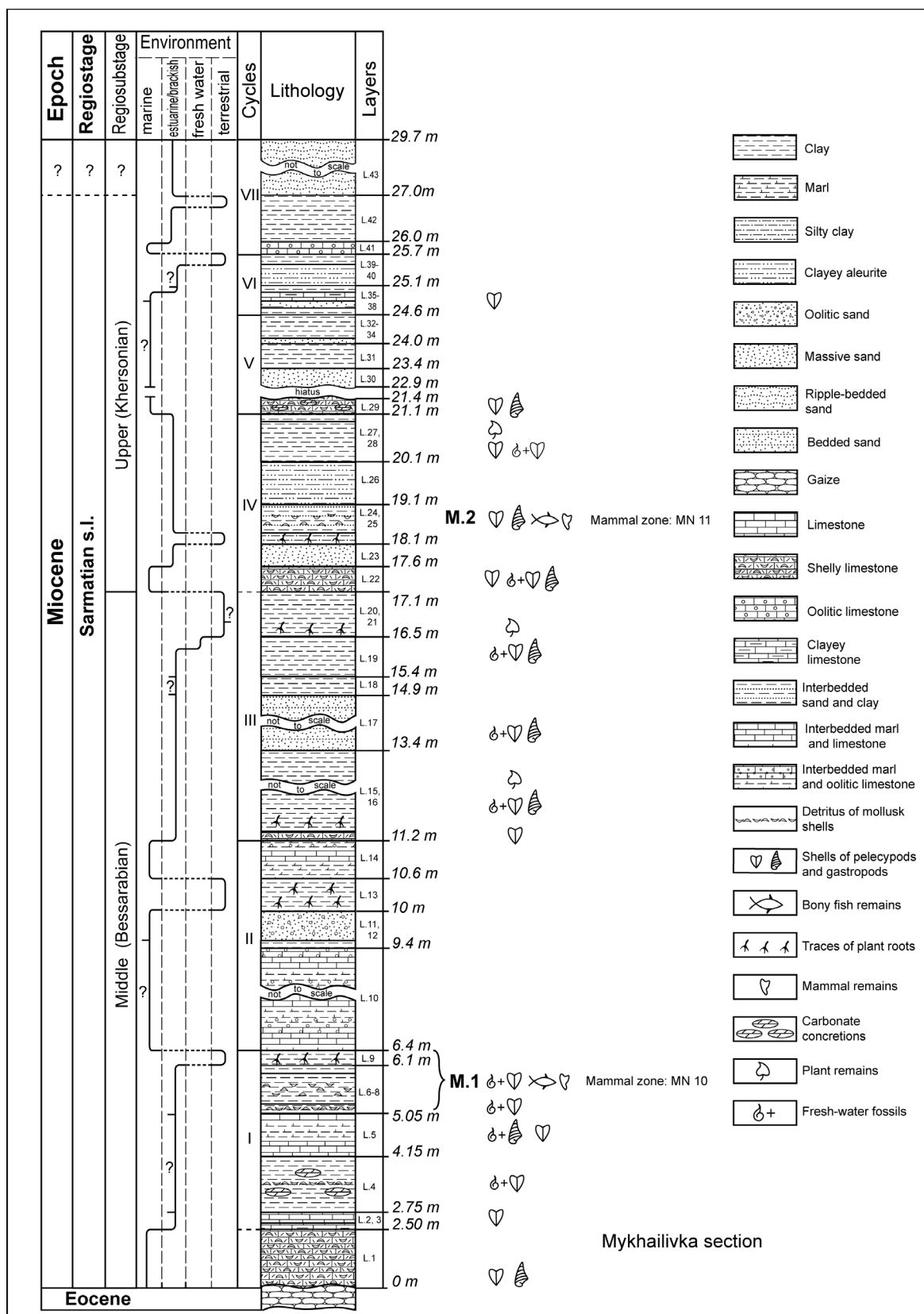


FIGURE 2. Stratigraphical position of the Mykhailivka section. Lithological and paleontological data from Prisyazhniuk et al. (2006). Reconstruction of environmental log deduced from Prisyazhniuk et al. (2006).

München (Germany). Photographs of otoliths were taken with a Leica M 165 FC stereomicroscope in the Department for Earth and Environmental Sciences, Palaeontology and Geobiology, Ludwig-Maximilians-Universität München. Terminology of otoliths follows Koken (1891), Weiler (1942) and Schwarzhans (1978, 2014). Abbreviations used: otolith length = OL, otolith height = OH.

SYSTEMATIC PALAEOONTOLOGY

Family MORONIDAE Jordan and Evermann, 1896

Genus *MORONE* Mitchell, 1814

Morone cf. *nobilis* (Koken, 1891)

Figure 3.1-4

- 1891 *Otolithes (Dentex) nobilis*; Koken, pl. 8, fig. 8.
- 1977 *Morone limburgensis* (Posthumus, 1923); Nolf, pl. 14, figs. 4-6.
- 1977 *Acropoma nobilis* (Koken, 1891); Nolf, pl. 15, figs. 21-22; pl. 18, figs. 3-4.
- 1994 *Morone nobilis* (Koken, 1891); Schwarzhans, figs. 373-388.
- 1996 *Acropoma nobilis* (Koken, 1891); Müller, pl. 5, fig. 7; pl. 7, figs. 17-18.
- 2009 *Morone nobilis* (Koken, 1891); Schwarzhans and Wienrich, pl. 199, figs. 4-6.
- 2010 *Morone nobilis* (Koken, 1891); Schwarzhans, pl. 73, figs. 6-12.
- 2013 *Acropoma nobilis* (Koken, 1891); Nolf, pl. 208.

Material. Two incomplete otoliths and one fragment (NMNHU-P 33/1482-1484, Mykhailivka 1).

Description. Otoliths are rather large (up to greater than 5 mm length). The anterior part of the ostium is damaged. The ventral rim is smooth and deeply curved, especially in the largest specimen (see Figure 3.1). The dorsal rim bears an antero-dorsal and a distinct postero-dorsal angle. The posterior tip is slightly rounded.

The inner face is convex; the outer face is slightly concave. The sulcus is situated slightly supramedian and is moderately deepened. The ostium is incomplete, but certainly was shorter than the cauda and is about twice as wide, and dorsally and ventrally expanded. The cauda is straight anteriorly, bent downward posteriorly and terminates at some distance from the posteroventral rim. The crista superior is distinct and sharp; the crista inferior is poorly expressed.

Remark. *Morone nobilis* is known from the late Oligocene and early to middle Miocene of the North Sea Basin (e.g., Koken, 1891; Schwarzhans, 2010). The specimens presented here are very similar, but are assigned to *M. nobilis* with some reservation because of their incompleteness and

the remoteness of the location from the North Sea Basin.

Family SCIAENIDAE Cuvier, 1829

Genus *GENYONEMUS* Gill, 1861

Genyonemus? sp.

Figure 3.5-8

Material. Two otoliths (NMNHU-P 33/1485, 1512, Mykhailivka 1).

Description. The elongate otolith is about 5 mm long, but its posterior part is not preserved. The ventral rim is smooth and anteriorly curved. The anterior tip is rounded. The dorsal rim is curved and slightly serrated with a broad median lobe, which is also slightly crenulated.

The inner face is faintly convex. The anterior part of the outer face is slightly concave and ornamented with many short radial furrows, while the posterior part is thickened and slightly convex. The sulcus is shallow with the cauda slightly deeper than the ostium. The ostium is three times wider than the cauda and is widened both dorsally and ventrally. The cauda terminates very close to the anterior rim of the otolith. The cauda is straight, only slightly bent posteriorly when approaching the posteroventral rim of the otolith. The crista superior is distinct.

Comparison. This otolith is very similar to the holotype of "genus aff. *Genyonemus*" *pertenuis* Müller, 1999 from the lower/middle Miocene of Eastern USA (Müller, 1999). It differs in the narrower cauda and more expressed postostial lobe. Rückert-Ülkümen (1996) described *Serranus acuterostratus* from Turkey, which may belong to the same genus as the ones from Mykhailivka. Our specimen, however, differs from *Genyonemus*? *acuterostratus* (Rückert-Ülkümen, 1996) in its anterior part being less elongate.

Family GOBIIDAE Cuvier, 1816

Genus *PONTICOLA* Iljin, 1927

Ponticola dorsorostralis (Weinfurter, 1954)

Figure 3.9-18

- 1954 *Gobius dorsorostralis* nov. spec.; Weinfurter, pl. 6, figs. 49-50.
- 1954 *Gobius dorsorostralis sculpta* n. sp., n. ssp.; Weinfurter, pl. 6, figs. 51-52.
- 1992 *Gobius* sp., aff. *Gobius dorsorostralis* Weinfurter, 1954; Brzobohaty, pl. 1, fig. 2.
- 2010 *Gobius dorsorostralis* Weinfurter, 1954; Schwarzhans, pl. 103, figs. 2-4.
- 2013 *Gobius dorsorostralis* Weinfurter, 1954; Nolf, pl. 320.
- 2014 *Gobius dorsorostralis* Weinfurter, 1954; Schwarzhans, pl. 8, figs. 1-2.

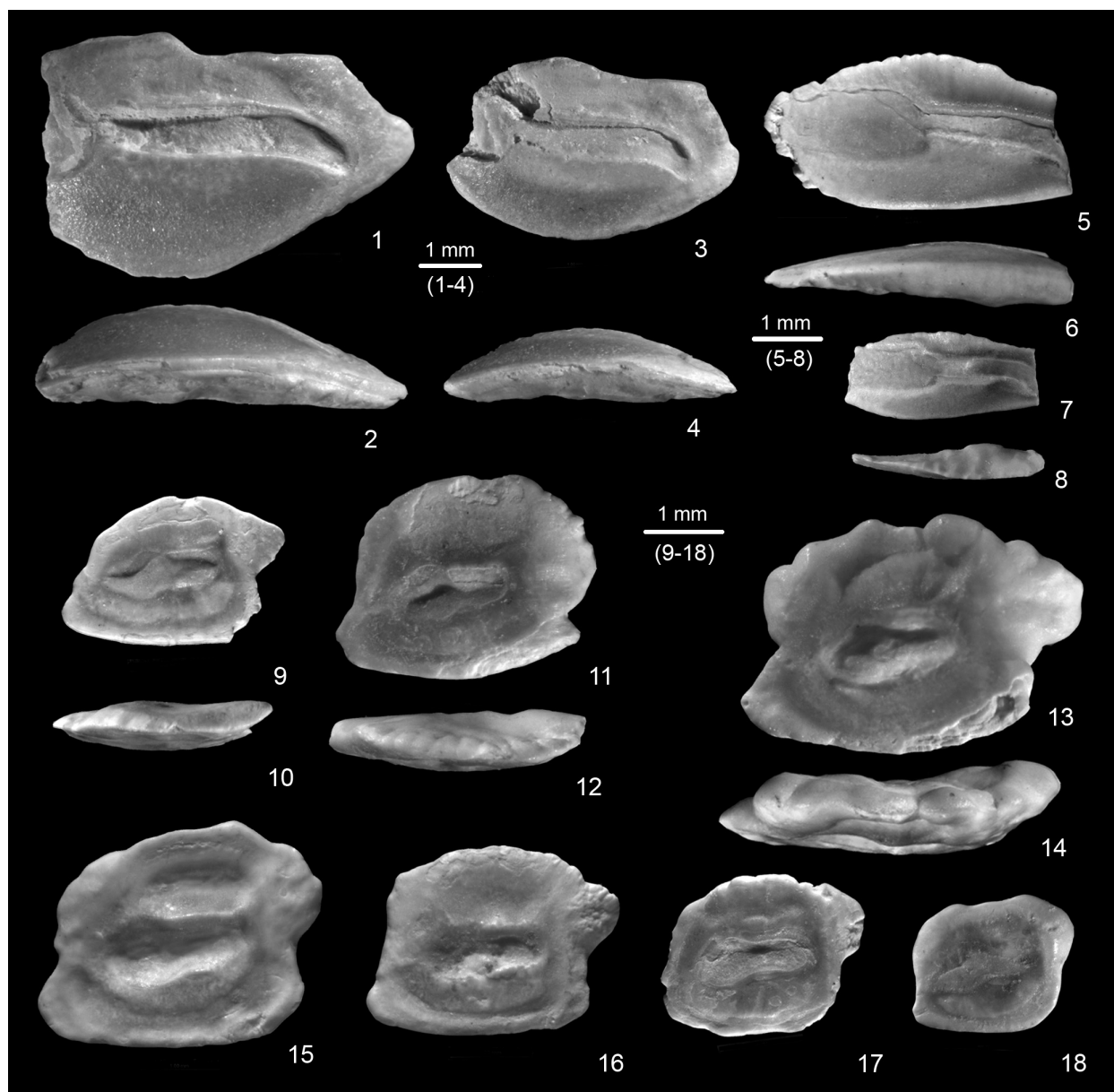


FIGURE 3. Otoliths from the Sarmatian s.l. of the Mykhailivka 1. **1-4**, *Morone* cf. *nobilis* (Koken, 1891): NMNHU-P 33/1482, inner face (**1**), ventral view (**2**); NMNHU-P 33/1483, inner face (**3**), ventral view (**4**). **5-8**, *Genyonemus?* sp.: NMNHU-P 33/1485, inner face (**5**), ventral view (**6**); NMNHU-P 33/1512, inner face (**7**), ventral view (**8**). **9-18**, *Ponticola dorsorostralis* (Weinfurter, 1954): NMNHU-P 33/1486, inner face (**9**), ventral view (**10**); NMNHU-P 33/1487, inner face (**11**), ventral view (**12**); NMNHU-P 33/1488, inner face (**13**), ventral view (**14**); NMNHU-P 33/1489, inner face (**15**); NMNHU-P 33/1490, inner face (**16**); NMNHU-P 33/1491, inner face (**17**); NMNHU-P 33/1492, inner face (**18**). Scale bars equal 1 mm. 5-10, 17, 18 are mirrored.

2014 *Gobius* aff. *dorsorostralis* Weinfurter, 1954; Schwarzhans, pl. 8, fig. 3.

Material. Ten otoliths (NMNHU-P 33/1486-1495, Mykhailivka 1).

Description. The rectangular otoliths are moderately elongate. Sizes range from 3 to 5 mm in length. OL:OH = 1.35-1.5. The anterior and posterior rims are inclined, slightly rounded, or straight.

They have pronounced anterodorsal and postero-ventral angles. The dorsal rim is slightly curved and intensely but irregularly undulating or sometimes deeply crenulated. The otoliths have a well-developed rounded (pointed in juveniles) posterodorsal projection. The ventral rim is nearly flat, and smooth with a well-expressed slightly pointed anteroventral projection. The otoliths are thin. The

inner face is slightly convex. The sulcus is sole-shaped with a gently pointed tip of the ostium. The latter is wider and longer than the cauda, although the distinction is fluent. There is no subcaudal iugum. The ventral furrow is well-expressed. Adult specimens, have a distinct dorsal depression. The outer face is slightly concave with some ornamentation and protuberances.

Comparison. This species is similar to several extant species of *Ponticola* in otolith shape and the lack of a subcaudal iugum (see Vasilieva et al., 2016). It is best recognized by the intensely ornamented dorsal rim and the moderate index of OL:OH.

Genus *NEOGOBIOUS* Iljin, 1927

Neogobius bettinae n. sp.

Figure 4.1-9

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Etymology. In honour of Bettina Reichenbacher (Munich, Germany) for her great contribution to the knowledge of fossil fish faunas, particularly freshwater fishes and gobioids.

Type material. Holotype: NMNHU-P 33/1496 (Figure 4.5-6). Paratypes: seven specimens NMNHU-P 33/1497-1503 (Figures 4.1-4, 4.7-9), Mykhailivka 1.

Type locality. Mykhailivka village, Mykolaiv region, Southern Ukraine.

Diagnosis. Compact otoliths with low anterodorsal rim and posteriorly elevated, rounded dorsal rim. Posterodorsal projection short, wide and rounded. Anteroventral projection weak or lacking. Sulcus with characteristic tip positioned just anterior to the junction of ostium and cauda. Otoliths rather thick (OH:OT = 2.0-2.2).

Description. The thick massive otoliths range from 1.5 to 4.5 mm in length. OL:OH = 1.16-1.23; 1.07 (in juveniles). The anterior rim is short with a weak or absent anteroventral projection. The posterior rim is vertical and can be incised beneath the posterodorsal projection. The dorsal rim is highly elevated posteriorly, curved and slightly undulating; the anterodorsal angle is very low. These otoliths have a broad, rounded posterodorsal projection, which gently bends outwards. The ventral rim is smooth and straight with a rounded posterodorsal angle. The inner face is gently convex. The deep sulcus is inclined and sole-shaped. The tips of the sulcus are rounded. The ostium is wider than the cauda and displays a distinct and often pointed lobe at the dorsal rim. Some specimens (Figures 4.1, 4.3, 4.5) have a faint and narrow subcaudal iugum, but in most instances it is missing. The crista superior is more pronounced than the crista

inferior. The ventral line is distinct. The dorsal depression is broad, distinct and rather deep in several specimens (e.g., Figures 4.5, 4.9). The outer face is slightly convex, with the greatest convexity at the long axis.

Comparison. Similar otoliths, showing the same characteristic tip of the ostial lobe, have been described from the middle Sarmatian of Azerbaijan as *Gobius pricaspicus* Pobedina, 1956 (see Pobedina et al., 1956, pl. 23, figure 4). Otoliths from the Mykhailivka locality are clearly different from those by having less crenulated rims, a depressed anterodorsal angle, and a distinctly longer sulcus. The faint or absent subcaudal iugum and the rather compressed shape with a low OL:OH index resembles Recent otoliths of the genus *Neogobius*. Otoliths of all extant species are figured here (Figure 5) for comparison [*Neogobius caspius* (Eichwald, 1831) (Figure 5.7-9), *N. fluviatilis* (Pallas, 1814) (Figure 5.5-6), *N. melanostomus* (Pallas, 1814) (Figure 5.1-2) and *N. pallasi* (Berg, 1916) (Figure 5.3-4)]. In the Recent species, *N. melanostomus* exhibits a clear subcaudal iugum, whereas in the other species it is either totally lacking or occasionally faint and indistinct as in *N. bettinae*. *Neogobius fluviatilis* and *N. pallasi* most closely resemble *N. bettinae*. However, *N. bettinae* is distinguished from the Recent species as well as the two fossil ones so far known (*N. rhachis* Rückert-Ülkümen, 1993 in Rückert-Ülkümen et al., 1993 and *N. udovi-chenkoi* Bratishko, Schwarzhans and Reichenbacher, 2015 [in Bratishko et al., 2015]) by the high postdorsal rim, the relatively short and broad postdorsal projection and the rather thick appearance (OH:OT = 2.0-2.2). Otoliths of extant *Gobius* species all show a distinct and broad subcaudal iugum except faint in *Gobius cobitis* and *G. paganellus*, which however have very slender otoliths. *Neogobius bettinae* differs from *N. rhachis* by the low anterodorsal angle and curved dorsal rim (vs. rather flat). Both species occur together in Mykhailivka, indicating an already advanced speciation of the genus in the Ponto-Caspian Basin, possibly including extinct lineages (see also Schwarzhans et al., 2017c).

Neogobius rhachis Rückert-Ülkümen, 1993 in
Rückert-Ülkümen et al., 1993
Figure 4.10-19

1993 *Neogobius rhachis* n. sp.; Rückert-Ülkümen et al., pl. 5, figs. 4-9.

2009 *Neogobius rhachis* Rückert-Ülkümen, 1993; Çevik Üner and Özkar Öngen, pl. 4, fig. 3.

Material. Eight otoliths (NMNHU-P 33/1504-1511, Mykhailivka 1).

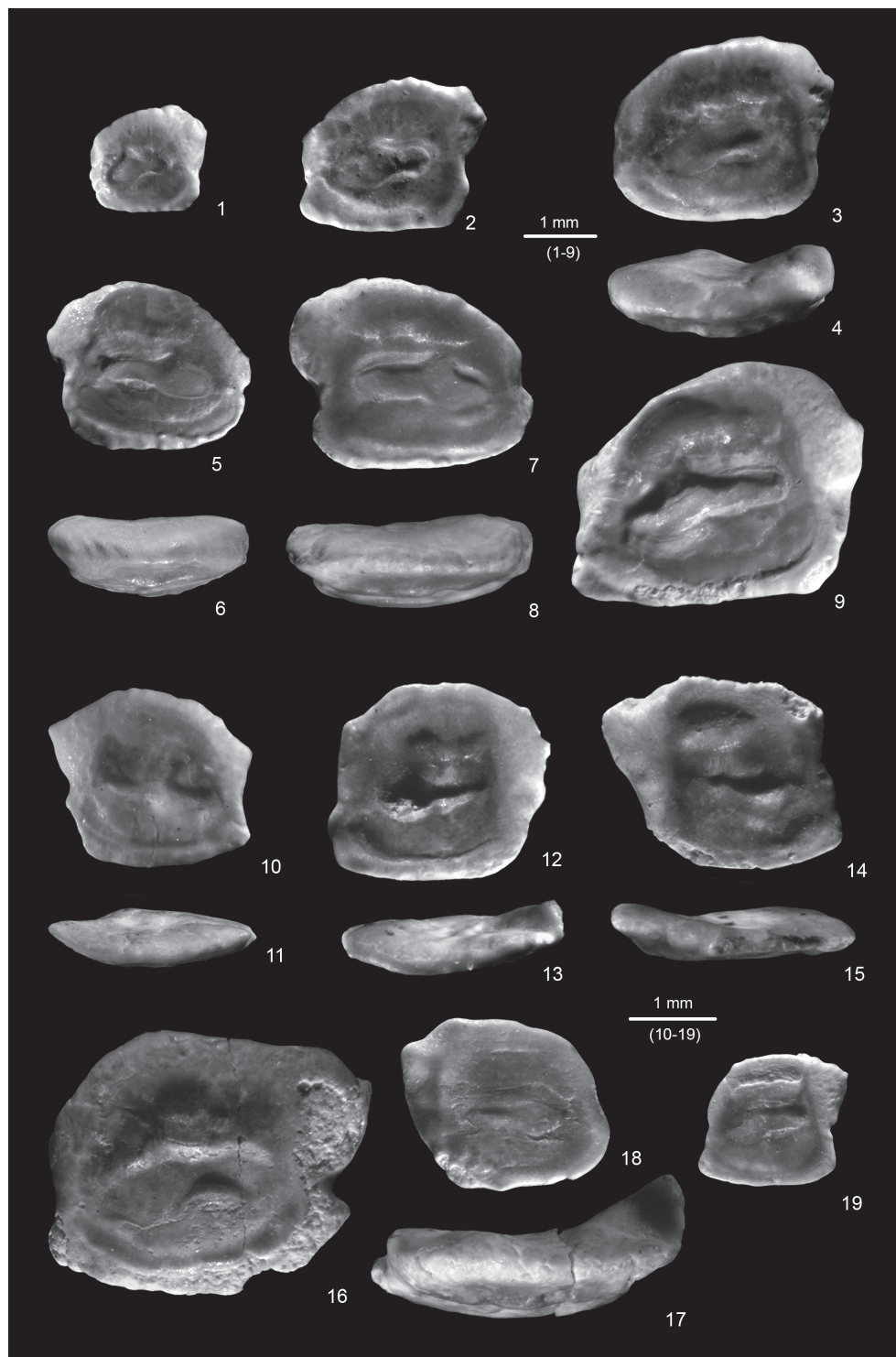


FIGURE 4. Otoliths from the Sarmatian s.l. of the Mykhailivka 1. **1-9**, *Neogobius bettinae* n. sp.: NMNHU-P 33/1497 (paratype), inner face (**1**); NMNHU-P 33/1498 (paratype), inner face (**2**); NMNHU-P 33/1499 (paratype), inner face (**3**), ventral view (**4**); NMNHU-P 33/1496 (holotype), inner face (**5**), ventral view (**6**); NMNHU-P 33/1500 (paratype), inner face (**7**), ventral view (**8**); NMNHU-P 33/1501 (paratype), inner face (**9**). **10-19**, *Neogobius rhachis* Rückert-Ülkümen, 1993 in Rückert-Ülkümen et al., 1993: NMNHU-P 33/1504, inner face (**10**), ventral view (**11**); NMNHU-P 33/1505, inner face (**12**), ventral view (**13**); NMNHU-P 33/1506, inner face (**14**), ventral view (**15**); NMNHU-P 33/1507, inner face (**16**), ventral view (**17**); NMNHU-P 33/1508, inner face (**18**); NMNHU-P 33/1509, inner face (**19**). Scale bars equal 1 mm. 5-8, 10, 11, 14, 15, 18 are mirrored.

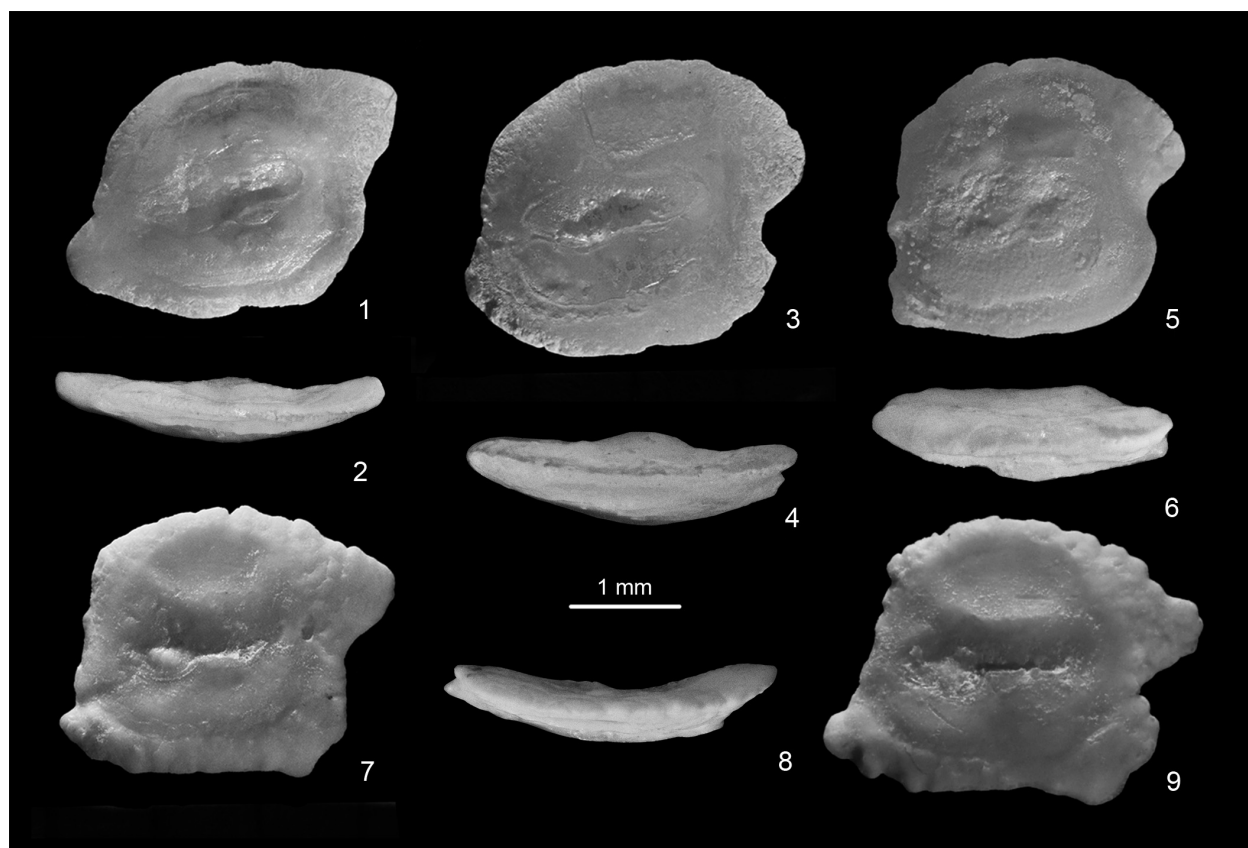


FIGURE 5. Recent otoliths of the genus *Neogobius*. **1-2**, *Neogobius melanostomus* (Pallas, 1814): ZMMU, P.23515 3, SL91, 43°38'N-51°08'E, inner face (**1**), dorsal view (**2**). **3-4**, *Neogobius pallasii* (Berg, 1916): ZMMU, P.23514, SL93, 43°28'N-51°18'E., inner face (**3**), dorsal view (**4**). **5-6**, *Neogobius fluviatilis* (Pallas, 1814): ZMMU, P.22433, SL81, 45°20'N-28°57'E, inner face (**5**), dorsal view (**6**). **7-9**, *Neogobius caspius* (Eichwald, 1831): **7-8**, ZMMU, P.22622 1, SL90, 51°25'N-46°03'E, inner face (**7**), dorsal view (**8**); **9**, ZMMU, P.22622 2, SL105, 51°25'N-46°03'E, inner face.

Description. These otoliths have a slightly tilted rectangular shape, and range in length from 2.0 to 3.5 mm. OL:OH = 1.1-1.26; OH:OT = 3.3-3.4. The anterior and posterior rims are oblique and almost parallel to each other. The posterior rim is steep and has a slightly rounded posteroventral edge. The dorsal rim is slightly curved; the wide, nearly triangular posterodorsal projection is somewhat bent outwards. The ventral rim is smooth and flat or slightly curved.

The inner face is only slightly bent, primarily along the postdorsal projection. The sulcus is moderately deep. It is sole-shaped and usually shows no subcaudal iugum or only a very narrow and small one. The ostial tip is rather angled, the caudal tip rounded. The ventral furrow is distinct. The dorsal depression is broad and shallow.

The outer face is slightly concave, particularly at the outwardly bent postdorsal projection, and has short radial furrows near the rims. The otoliths are thinner along the dorsal part and increase in

thickness towards the ventral part. The postdorsal projection is supported by a ridge on the outer face.

Comparison. *Neogobius rhachis* differs from *N. udovichenkoi* Bratishko, Schwarzhan, and Reichenbacher, 2015 from the Konkian of Mangyshlak (Kazakhstan) in having a more compressed outline expressed in the smaller index of OL:OH (1.10-1.26 vs 1.2-1.4) and shorter pre-ventral and posterodorsal projections. The slightly oblique, parallel anterior and posterior rims represent a characteristic feature for *N. rhachis* as well as the ridge on the outer face supporting the postdorsal projection. Furthermore, *N. rhachis* is very similar to otoliths of the extant *N. fluviatilis* (Pallas, 1814) (Figure 5.5-6), which is common in the rivers flowing to the Azov and Black Seas (Froese and Pauly, 2016). Nevertheless, otoliths of the fossil species are thinner and have a more pronounced and bent posterodorsal projection.

DISCUSSION

Palaeoecological Analysis

Fossils obtained from the marl-clayey deposits of the Mykhailivka 1 level (Figure 2) contain abundant freshwater molluscs (*Anisus*, *Valvata*, *Hydrobia*), and rare marine (*Mactra*) and terrestrial (*Carychium*, *Vertigo*, *Gastrocopta*) molluscs (Prisyazhniuk et al., 2006). Brackish ostracods (*Cypri-deis*) dominate in Mykhailivka 1: layers 6, 7 have more than 80%, and layer 8 has 45% (plus up to 50% of freshwater ostracods), while the portion of marine specimens is small (Prisyazhniuk et al., 2006). Pharyngeal teeth and bones of fishes are represented primarily by cyprinid genera in Mykhailivka 1: *Scardinius*, *Palaeocarassius*, *Luciobarbus* and *Tinca*. They are interpreted to be indicative of a river system with extensive small tributaries and with warm slowly-flowing low energy freshwater, with a muddy bottom and thickets of underwater vegetation (Kovalchuk, 2015). The entire sedimentary sequence at Mykhailivka was probably deposited near the former coast line of the Eastern Paratethys and is characterized by ephemeral shallow marine incursions, probably in an estuarine setting.

The fish otoliths studied here do not represent any of the fish groups represented by teeth or bones, but rather complement the faunal association. Otoliths have been identified representing three different families: Moronidae, Gobiidae and Sciaenidae. *Morone* is an anadromous, demersal fish, living in small shoals in coastal marine and estuarine habitats and is regularly invading nearby brackish and freshwater bodies. It is also known from quiet water areas of medium to large rivers with mud bottoms (Froese and Pauly, 2016).

The Gobiidae are an extremely diverse, widely distributed and successful shallow water marine, brackish and freshwater family with many euryhaline species (Froese and Pauly, 2016). *Ponticola dorsorostralis* is known from brackish deposits of the Pannonian (Tortonian) of the Vienna Basin (Weinfurter, 1954) and the Sarmatian s.s. (Serravallian) of Wiesen in Austria (Schwarzhans, 2010). Otoliths identified as *Gobius* aff. *dorsorostralis* from the Karaman Basin in Turkey were also recorded from brackish-marine deposits (Schwarzhans, 2014). Our material confirms the conclusion of Schwarzhans (2014) that *P. dorsorostralis* possibly was a non-marine species. *Neogobius rhachis* was originally described from the Sarmatian s.s. to Pannonian in freshwater to brackish environments of the southwestern part of the Eastern Paratethys

in Western Turkey (Rückert-Ülkümen et al., 1993). Finally, *Neogobius bettinae* is here recorded for the first time. It is interpreted as related to the extant *N. fluviatilis*, which is a fresh- to brackish water species of the tributaries of the Ponto-Caspian Basin. All three gobiid species at Mykhailivka thus represent the endemic Ponto-Caspian goby group, which has adapted so successfully to the changing environments and water salinities of the basin since the Sarmatian times of the Paratethys (Schwarzhans et al., 2015, 2017c). None of these species has been recorded from the rich stenohaline marine gobiid faunas of the Sarmatian of the Paratethys. The Sciaenidae, finally, are well known for their adaptation to the warm shallow seas and estuaries of the world, both in the Recent (Trewavas, 1977) as well as the fossil record (Schwarzhans, 1993; Aguilera et al., 2016). Many of the species occurring in estuarine environments are also known to move up river into brackish and freshwaters (Aguilera et al., 2016).

We therefore conclude that the fish fauna from the Mykhailivka 1 level matches with a mixed – freshwater and brackish, probably estuarine – environment, which was also favorable for anadromous species. Other paleontological data and the lithological sequence confirm a close proximity to a large marine basin, i.e., the Eastern Paratethys, in a riverine and estuarine setting with low to moderate energy.

The fossil assemblage of the Mykhailivka 2 level (Figure 2) did not contain otoliths. The basal level of the layer contains shells of marine, and freshwater, as well as terrestrial molluscs according to Prisyazhniuk et al. (2006). They also observed certain freshwater clams, i.e., *Pseudohyriopsis* and *Potamoscapha*, *in vitro*. The ostracod fauna from layers 22, 23, 25, and 26 (Figure 2) comprises variable amounts of marine (from 10% to 80%) and brackish (from 20% to 80%) taxa with minor (less than 5%) numbers of freshwater specimens (Prisyazhniuk et al., 2006).

The fish assemblage of layer 25 contained pharyngeal teeth and bones (but no otoliths), which are all from typical freshwater fishes and could represent the next step in the development of the regional set-up located in the lower part of the river system at some distance from the sea. Kovalchuk (2015) interpreted the faunal elements to indicate the presence of nearby rapids with cold water (*Chondrostoma*, *Luciobarbus*), slowly flowing water (*Esox*), overgrown warm ponds (*Palaeocarassius*, *Tinca*), and backwaters (*Silurus*) all in the lower reaches of the river (Kovalchuk and Ferraris,

2016). The reason for the absence of otoliths of these fishes from both Mykhailivka 1 and 2 is not yet understood. However, Mykhailivka 2 entirely lacks otoliths including any indication of moronid, goby, and sciaenid otoliths found in Mykhailivka 1.

Palaeogeography and Biostratigraphy

The limited amount of otolith-based taxa allows only a limited evaluation of the palaeogeography and biostratigraphy of Mykhailivka 1.

Morone cf. *nobilis* from Mykhailivka 1 is the first record of this species in the Eastern Paratethys, and it is probably also the youngest record of the species. Schwarzhans (2010) recorded *Morone nobilis* as common and widespread in the North Sea Basin, ranging from the Chattian to the lower Langenfeldian (late Serravallian). There are no earlier records of *M. nobilis* in the Central or the Eastern Paratethys despite a relatively good fossil otolith record. Therefore, its occurrence in Mykhailivka requires some sort of connectivity among these regions about which we feel unable at present to speculate. It should be noted, however, that Schwarzhans et al. (2017b) reported a case of a typical, putatively endemic Paratethyan gadid, *Paratrisopterus caspius* Bogatshov, 1929, possibly also occurring in the late Miocene of the North Sea Basin.

Neogobius rhachis clearly confirms the connections of the former Galician Gulf with the brackish/freshwater lakes of Western Anatolia (Rückert-Ülkümen et al., 1993; Popov et al., 2004). *Ponticola dorsorostralis* indicates the connectivity between the freshwater/brackish water regions of the Central and Eastern Paratethys during the middle Sarmatian s.l. Interestingly, the Mykhailivka 1 otolith assemblage does not have any species in common with the very rich coeval otolith-based fauna of Jurkino, Kerch Peninsula (Bratishko and Schwarzhans, unpublished data) despite the rather close proximity. From preliminary data, the Jurkino fish association is very rich in gobiids although these all represent different species from those of Mykhailivka. The reason for this faunal difference clearly is related to the difference in environment: fully marine, albeit with a somewhat reduced salinity at Jurkino, and riverine to estuarine at Mykhailivka.

The small fish fauna obtained from Mykhailivka thus represents a still rare window into the freshwater fish fauna of the Sarmatian / Ponto-Caspian borderland, one of the largest and most dynamic freshwater bioprovinces of Eurasia.

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